

THE BIOLOGY AND ABORIGINAL USE OF THE HONEYPOT ANT, *CAMPONOTUS INFLATUS* LUBBOCK, IN NORTHERN TERRITORY, AUSTRALIA

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Abstract

Three Earthwatch expeditions excavated two nests, plotted colony distribution and observed foraging of the honeypot ant, *Camponotus inflatus*, in Northern Territory, Australia in July-August, 1987. Nests were associated with mulga trees (*Acacia aneura* F. Muell. ex Benth.) and had either single or multiple entrances. Two colonies contained 1063 and 4019 ants. Workers with swollen abdomens, called repletes, comprised 49% (516) and 46% (1835), respectively, of the populations. Six wingless queens were in the smaller colony. Replete abdomens were clear to dark amber; the largest was 15 mm long and weighed 1.4 g. The larger colony had 66 replete chambers with up to 191 repletes per chamber, reached a depth of 1.7 m, and radiated as far as 2.4 m from the entrance. Honeypot ants foraged during the day at extrafloral nectaries on mulga phyllodes as far as 9 m from nests and on a blue-tongued lizard (*Tiliqua* sp.) carcass. A raid of one honeypot ant colony on a smaller colony lasted several days and involved interactions with four ant species. Honeypot ants are eaten by some Aboriginal people and are significant in their Dreamtime, culture, and livelihood.

Introduction

The Australian ant fauna is among the richest and most diverse in the world, particularly in semiarid regions, but there is little information concerning the biology of many species, such as the black honeypot ant, *Camponotus inflatus* (Taylor, 1972; Greenslade and Greenslade, 1989; Andersen and Yen, 1985).

Many ants forage for nectar (Cleland, 1965; Tindale, 1961), and/or honeydew, but honeypot ants store these secretions in the crops of certain swollen workers, repletes, hanging from domed chambers in the nest. This behaviour culminates in two Formicinae, *C. inflatus* in Australia and *Myrmecocystus mexicanus* Wesmael in North America, in which repletes develop abdomens the size of grapes (Greenslade, 1979; McCook, 1882). These species have undergone convergent evolution, independently developing the same adaptation to store transient nectar supplies in a semiarid environment.

C. inflatus appears to have a widespread but patchy distribution over the arid interior: from Hooker Creek in the Northern Territory to the Murchison in Western Australia to the Everard Range in South Australia (Spencer and Gillen, 1899; White, 1915; Basedow, 1925; Spencer, 1928; Bicchieri, 1972; Gould, pers. comm., 1987). This species is usually associated with mulga trees (*Acacia aneura*) which provide nectar, insect prey, and shelter from high temperatures and evaporation (Low, 1978).

The purposes of our study were to determine nest density, foraging distances, food sources and intra- and interspecific interactions.

Careful excavations provided information on nest architecture, population size, and repletes. We worked with Aborigines to learn about the significance of this ant in their diet and culture.

Materials and methods

Three Earthwatch expeditions studied *C. inflatus* in the Northern Territory of Australia in July-August 1987. Two expeditions worked at Kunoth Paddock, a small part of the Hamilton Downs Cattle Station, 50 km north-west of Alice Springs. This site was chosen because it contains numerous honeypot ant nests (including a number previously excavated by Aborigines) and had been mapped and studied. It is tall shrubland consisting of perennial mulga on red sandy loam at an elevation of 683-710 m. The climate is arid to semiarid with an average rainfall of 263 mm. Most work occurred in July, the coldest month, which has average maximum and minimum temperatures of 19°C and 4°C (Low, 1978).

Colony distribution and foraging were assessed by mapping nests on one hectare and marking some workers with acrylic paint. We determined one nest's architecture by centring a north-south, east-west string grid over its entrance and recording the depths and dimensions of passages and chambers in each quadrant excavated. Nest and ground temperatures were measured with a digital thermometer. All ants were collected. We weighed 277 repletes on a balance and measured their abdominal lengths.

A *C. inflatus* nest was also excavated 3.8 km from the Ranger Station in Uluru National Park (Ayers Rock) and the coordinates and depths of passages and chambers recorded. All ants were collected and 503 repletes weighed in the field with a spring balance and their abdominal lengths measured with calipers.

To learn how Aborigines use honeypot ants I camped with a family near Alice Springs, worked with guides at Uluru National Park, and interviewed women at the Institute of Aboriginal Development in Alice Springs.

Results

The density of *C. inflatus* nests at Kunoth is 24-26/ha, but was difficult to determine with certainty since some were inactive and/or partially excavated by Aborigines. There were 16 active nests; 6-7 excavated inactive nests; and 2-3 probable nests based on worker activity in the vicinity. Minimum distances between nests ranged from 5 m between active nests to 2.4 m between active and inactive nests. Six nests were 0.2-1.7 m away from mulga trees.

The entrance to the excavated Kunoth nest was 2.5 x 3.8 cm. Another nest had two entrances 4-5 cm apart, but one was more active. Excavation of the Uluru nest uncovered four passages leading to the

surface 18 to 55 cm from the entrance suggesting that either the entrance changed position over time or that multiple entrances had been present.

Little is known about the subsurface architecture except Froggatt's (1896) description of the entrance leading into a 5-6 foot vertical shaft going to a large chamber at the bottom with a number of honeypot ants. He also noted horizontal foot-long passages containing 3-4 honeypot ants which lead off the main shaft about a foot below the surface. Our excavations provide a more detailed picture of the nest. The Kunoth nest radiated from the entrance 2.4 m SW, 1 m SE, 1 m NE, and 0.4 m NW, and reached a depth of 1.7 m. The shallowest passage was 1.9 cm deep. Repletes were in 66 chambers 0.2 to 1.7 m deep. The number per chamber ranged from 1-191, an average of 28 per chamber. Refuse middens, some containing dead honeypot ants and pupal cases, were in a passage 5.7 cm deep and rooms at 1 m and 1.7 m. Nest temperatures ranged from 9.4-17.2°C.

The smaller Uluru nest radiated 0.95 m SW, 1.3 m SE, 1.1 m NE, and 1.8 m NW, and reached a depth of 0.54 m. The shallowest passage was 3.5 cm deep. Repletes were in 16 chambers 26 to 54 cm deep with 1-125 per chamber, an average of 31 per chamber. The largest chamber was 18 cm long, 15 cm wide and 3 cm high. Another small honey ant colony, *Plagirolepis* sp., was found 0.95 m south-west from the *C. inflatus* entrance with three replete chambers at depths from 26-42 cm.

Although the Kunoth and Uluru nests differed greatly in size, both radiated asymmetrically from the entrance and had widely scattered dome-shaped chambers off several vertical passages. Some chambers were separated by only 1-2.5 cm from the ones below. Both nests extended into the root zones of nearby mulgas.

The populations of the excavated nests varied considerably. The Kunoth nest housed 4019 ants: 1835 repletes and 2184 workers. Numerous small larvae (652 counted) and large larvae (11 counted) were at depths from 17.5 cm-1.7 m. The Uluru population was 1063: 516 repletes, 541 workers, and 6 wingless queens (3 physogastric). Larvae were also present. Eggs, pupae, external parasites and myrmecophiles were absent from both nests.

I observed *C. inflatus* feeding on one blue-tongued lizard (*Tiliqua* sp.) carcass about 0.6 m from a nest entrance. We also observed honeypot ants foraging on one or more mulga trees 1.8 to 9 m from their nests between 0925 and 1500 h at Kunoth Paddock at ground temperatures of 12-30°C. They chewed and scraped front tarsi on mulga 'leaves' (phyllodes) and drank the exudate and licked yellow bud-like structures, but they usually drank from single, sunken extrafloral

nectaries at the base of phyllodes (Cleland, 1965). Only one forager developed a swollen abdomen.

Various substances were given to honeypot ants to determine food preferences and observe trophallaxis. Workers and repletes fed on bee honey and lerps, but not on dilute bee honey, sugar water or a disabled cricket. Only one worker developed a swollen abdomen. Regurgitation was observed between repletes, workers, and a worker and a replete.

We noted intraspecific hostility on two occasions at Kunoth Paddock. On 5 August a worker 3.8 m from her nest fought a honeypot ant from another colony. They used their mandibles and sprayed acid from abdomens slung forward beneath their bodies.

The second instance involved a raid by a large honeypot ant colony on a small nest 4.5 m away. The battle may have resulted from the establishment of a new colony in the territory of the larger nest. Fighting was first observed about noon on 16 July in an area 40 cm by 40 cm around the small nest entrance. Since no brood or repletes were carried away, it was probably not a slave raid (Holldobler, 1976). The battle diminished as the afternoon progressed, but resumed at 0930 the next day when 63 dead ants were collected. On 18 July the raiders left their nest for battle at 0915 but 20 minutes later some were also on a mulga tree.

Four ant species entered the battle area between July 16-21. *Rhytidoponera* sp. workers from nests 12.6 m and 31.1 m away fought each other and honeypot ants and carried off their remains. Encounters between *Camponotus denticulata* Kirby soldiers from a slit-entrance nest (Greenslade, 1979; Spencer, 1928) 8.2 m away and honeypot ants led to some fatalities, but often resulted in sprayed soldiers staggering away and wiping their heads. Two smaller unidentified ant species, one from a nest 2.4 m away, also carried away dead honeypot ants.

We observed the common Aboriginal practice of eating repletes ("tjala") singly by holding the head and thorax between two fingers and biting off the distended abdomen (Froggatt, 1896; Winfield, 1982; Bryce, 1986; Devitt, 1986). This method is identical to the use of *Myrmecocystus* repletes by Indians of the American Southwest and Mexico (Curran, 1937; De Conconi and Moreno, 1979) and indicates convergent evolution of their utilization by native peoples on both continents. Australian and North American repletes have a flavour like cane molasses, but often have an acrid aftertaste due to formic acid. Aboriginal women at Uluru told me that if a large number are eaten without water, the effect is like drinking too much wine - your head feels funny, your belly burns, and you feel dry inside and need to drink a lot of water.

The continued use of honeypot ants by Australian Aborigines provides insights into how they might have been utilized by North American Indians. We were told that Aboriginal women usually gather honeypot ants, a skill taught to young girls by senior women. We found 26 Aboriginal excavation pits at Kunoth Paddock; one to three associated with each nest. The digs covered areas of 0.09-5.72 sq. m (\bar{x} = 1.1) and ranged in depth from 10-100 cm. Partial excavations appear to be common and may preserve the species since queens, workers and brood move down when a colony is disturbed.

Discussion

A major question is why honeypot ants occur in some patches of mulga and not others. Nelson (pers. comm., 1987) believes honeypot ants only thrive in undisturbed mature mulga stands and are abundant at Kunoth Paddock because cattle do not enter this area. Other factors, such as temperature, humidity, soil type, predation and availability of nectar and honeydew may also determine distribution.

Honeypot ants may protect mulga trees. Lamont (1979) reports extrafloral nectaries may be universal in *Acacia* of south-western Australia, where their year round secretion attracts ants to defend nectaries, or the whole plant, against herbivores (Buckley, 1982). We only observed one *C. inflatus* worker eating a small red insect or mite on a phyllode, but Aboriginal women said grubs ("muyamuya") on mulga leaves are fed to honeypot ant larvae. We did see workers move along the length of each phyllode, the same foraging pattern used by other ants to detect insects on acacia (Majer, 1979; New, 1984).

It is questionable whether extrafloral nectaries alone could sustain a honeypot ant colony since their secretions are not abundant and contain mainly glucose and fructose which do not provide a complete diet (Buckley, 1982). Further study is needed to determine whether the interaction between *A. aneura* and *C. inflatus* involves obligate mutualism and co-evolution similar to other ant-plant associations.

Honeypot ants are reported to get nectar from a variety of sources at other times of the year. Mulgas provide nectar when they flower at the end of August (Bicchieri, 1972; Hart, 1974; Nelson, pers. comm., 1987). Morton (pers. comm., 1986) believes ants use spring-flowering shrubs, such as *Cassia*, and Aboriginal women at Uluru said repletes store nectar from black corkwood blossoms (*Hakea* sp.), red *Eremophila latrobei* flowers ("mintjingka"), and yellow mulga flowers ("inuntji"). Others report honeypot ants gather nectar from the "mulga apple," an acacia gall (Basedow, 1904; Spencer, 1928; Mckeown, 1944).

Primary 'honey' sources for *C. inflatus* may be 'lerps' (sugary scales secreted by psyllids) and scale insects (Coccidae) (Spencer, 1928; Kean,

1987) which cover mulgas for about three weeks in the spring (Latz, pers. comm., 1984). Lerps infest the bark and leaves and exude clear droplets, especially after rain (Bryce, pers. comm., 1987). Bicchieri (1972) reports lerp infestations over large areas of *A. aneura* but not in other areas; one factor which might contribute to this ant's discontinuous distribution.

Replete abdomens range in colour from clear to dark amber as in *Myrmecocystus mexicanus*, but the clear to clear-amber ones are few in number (19 of 277 Kunoth repletes) (Conway, 1977, 1990a). These colour variations, which have also been reported by Aborigines (Devitt, 1986), may be due to different storage products. Dark amber repletes store fructose and glucose (Basedow, 1904; Badger and Korytnyk, 1956; Conway, 1977) and clear ones may store water (Snelling, 1976). Australian repletes reach larger sizes (15 mm gaster; 1.4 g) than *M. mexicanus* repletes (12 mm gaster; 0.98 g) (Conway, 1990 a, b).

I saw no evidence of predation on honeypot ants and Jakamara, my Aboriginal guide, said the nests are not dug out by mammals as sometimes occurs in Arizona (Chew, 1979; Conway, 1990a).

Froggatt (1896) mentions extensive Aboriginal excavations of honeypot ant nests around Ayers Rock. Aborigines still expend much time and effort locating and excavating nests but most digs are partial and last less than an hour (Devitt, 1986). Others have reported digs as deep as 1.2-1.8 m (Spencer, 1928; Hart, 1974; Winfield, 1982) and several meters in diameter (Bicchieri, 1972). Honeypot ants were originally sought by Aborigines as a sweet, but now the digging is often a picnic with a purpose, a mother teaching children their way of life with its values and customs (Hart, 1974).

Honeypot ants also play a role in Aboriginal mythology. Aborigines believe all creatures and topographical features result from the activities of their totemic ancestors during the Dreamtime. Each animal and plant has a 'Dreaming' - the story of its creation and importance. I was told the totems and ceremonies associated with honeypot ants are still extant at Aboriginal settlements such as Papunya and Yuendumu north-west of Alice Springs.

Honeypot ants also have commercial importance. Honeypot ants have been depicted by Aborigines for thousands of years in ground mosaics and cave paintings. Today Aboriginal paintings on canvas, as well as T-shirts and postcards depicting honeypot ant dreaming are sold to tourists. Thus, honeypot ants still play an important role in the diet, Dreamtime and livelihood of Aboriginal people (Hart, 1974; Devitt, 1986).

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